BREEDING OF EIGHT SYMPATRIC SPECIES OF *PHYLLOSCOPUS* WARBLERS IN KASHMIR[1]

TREVOR PRICE[2] AND NITIN JAMDAR[3]

(With five text-figures)

INTRODUCTION

Many ecologists have asked what affects the number of species in a community and what affects their ability to coexist. These questions are of obvious importance in the context of species preservation. Among birds, competition for food has been thought to be very important in affecting which species could coexist in a given area (Cody 1974), but in the breeding season other factors, such as nest predation (Martin 1988a, in press) and periods of sporadic food shortage outside the breeding season (Wiens 1977) and are now given a prominent role.

A basic tenet of the competition hypothesis is that ecologically identical species cannot continue to coexist. Various alternative hypotheses are therefore best examined in situations where apparently ecologically very similar species do coexist. Thus, MacArthur (1958) showed that similar species of North American warblers partitioned the foraging habitat in subtle ways during the breeding season. Lack (1971) reviewed this study, and noted that the coexistence of such similar species is extremely rare, and identified no comparable situations in Europe.

We have discovered a situation which may be similar to that studied by MacArthur (1958). Eight species of warblers in the genus *Phylloscopus* breed in the mountains surrounding the Vale of Kashmir (Ali and Ripley 1983, Price and Jamdar 1990). All species are common, and some are abundant. The species are very similar. In this paper we describe the similarities and differences among the species with respect to their breeding biology. We concentrate on adding to, and correcting previous knowledge about these birds in Kashmir, as summarised in Hume and Oates (1889), Osmaston (1927), Baker (1933), Bates and Lowther (1952), and Ali and Ripley (1983). A future paper will deal in more detail with ecological differences between the species (Price in prep.).

METHODS

This study was conducted from May through July of each year 1985- 1987 at the Overa Wildlife Sanctuary, near Pahalgam, Kashmir. A full description of the locality and methods used are given by Price and Jamdar (1990). The Sanctuary spans an altitudinal range from *c.* 2400 to *c.* 4400 m. Three distinct habitats are occupied by the warblers: the coniferous woodland, and associated deciduous trees in clearings and along valleysides (*c.* 2400 to *c.* 3100 m), the birch woodland (interspersed with conifers and rhododendrons) from *c.* 3100 to *c.* 3600 m, and juniper bushes which lie above the birch.

We spent most of our time camped at two localities named UP1 and UP2 at about 3300 m in the birch woods, but also frequently visited areas at 2400 m and 2800 m in and beside the fir woods (Price and Jamdar 1990). Much of the data we report here were collected during an intensive study of one of the *Phylloscopus* species, the yellowbrowed leaf warbler *P. inornatus* (Price and Jamdar 1991). Quality of the data varies greatly among species, and is fragmentary for the rarer species.

Many individuals were trapped in mist nets, measured, and ringed. We measured wing-

[1]Accepted February 1990.

[2]Dept. of Biology C-016, University of California at San Diego, La Jolla, CA 92093, U.S.A.

[3]Samata, Gen. Bhosale Marg, Bombay 400 023.

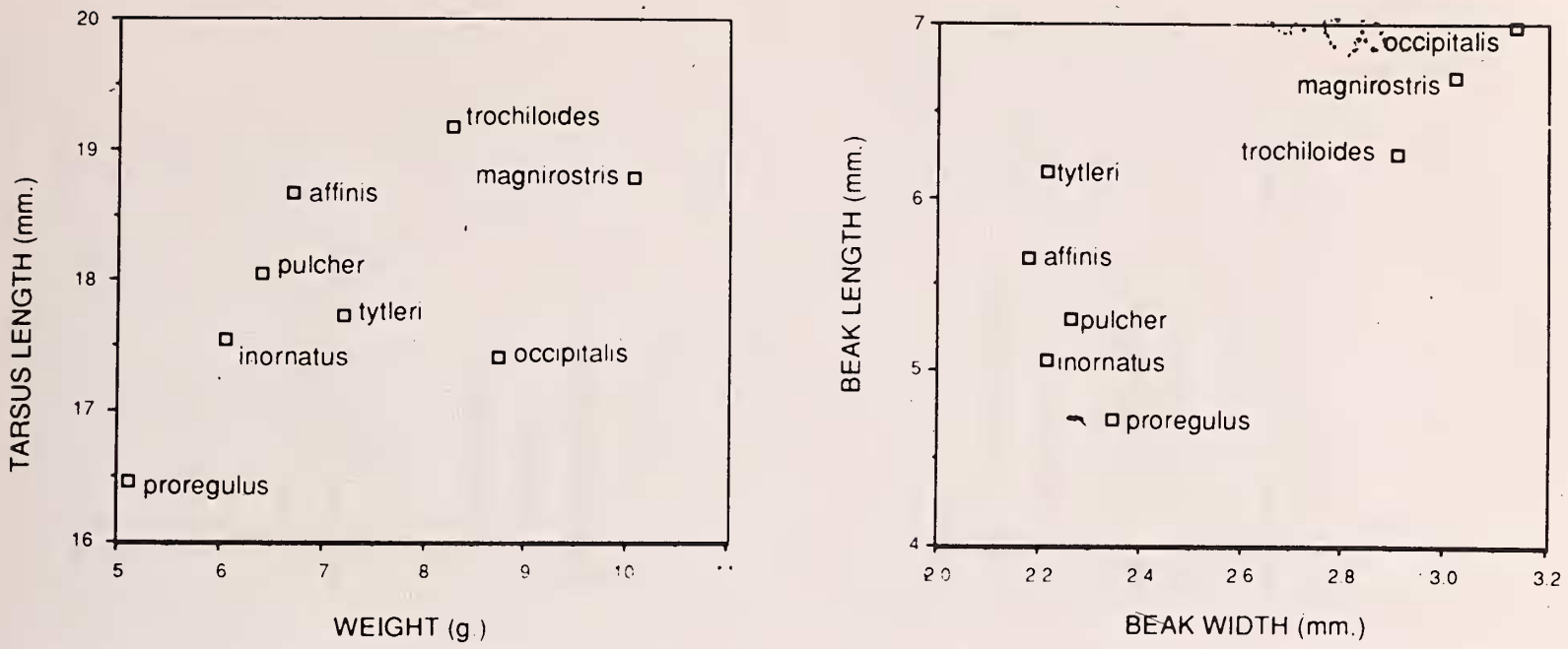

Fig. 1. Scatter plots of tarsus length against body weight, and beak length against beak width for the 8 species. Measurements from Table 1.

length to the nearest mm using the maximum chord method described by Svensson (1984) and weight to the nearest 0.1 g using a spring balance. Beak width and beak depth were measured to the nearest 0.1 mm in the plane of the anterior end of the nares using callipers. Beak depth was measured with the callipers held perpendicular to the commisure. Beak length (to the nearest 0.1 mm) was measured from the front of the nares to the tip of the bill using a pair of dividers. Although in all species the sexes look similar we were able to sex some birds. First we caught singing males by playing back tape-recorded songs. Second, only females incubate in all the species, and hence they can be sexed by the presence of a brood patch. This meant that when we trapped parents at their nest both the female and male could be sexed.

We observed birds in the field, and recorded breeding behaviours whenever possible. At intervals particularly in 1985 and 1986, we conducted a 2 km post-dawn walk along a valley in coniferous forest at *c.* 2500 m altitude, and recorded all warblers we heard singing. Whenever possible we searched for nests of all species, and recorded nest locations and contents and timing of breeding.

TABLE 1
EXTENT OF TERRITORY OVERLAP AMONG SPECIES

	tytleri	*affinis*	*pulcher*	*inornatus*	*proregulus*	*magnirostris*	*trochiloides*	*occipitalis*
tytleri								
affinis	N							
pulcher	N	N						
inornatus	O	A	O					
proregulus	P	N	A	P				
magnirostris	P	N	N	P	A			
trochiloides	N	A	O	O	N	A		
occipitalis	P	A	P	O	O	O	N	

O–Total overlap recorded: one species' territory has been recorded completely contained within the other's. P–Partial overlap recorded: one species' territory has been recorded overlapping part of the other's. A–No clear cases of territory overlap, but territories have been recorded abutting one another. N–Cases of adjacent or overlapping territories never recorded.

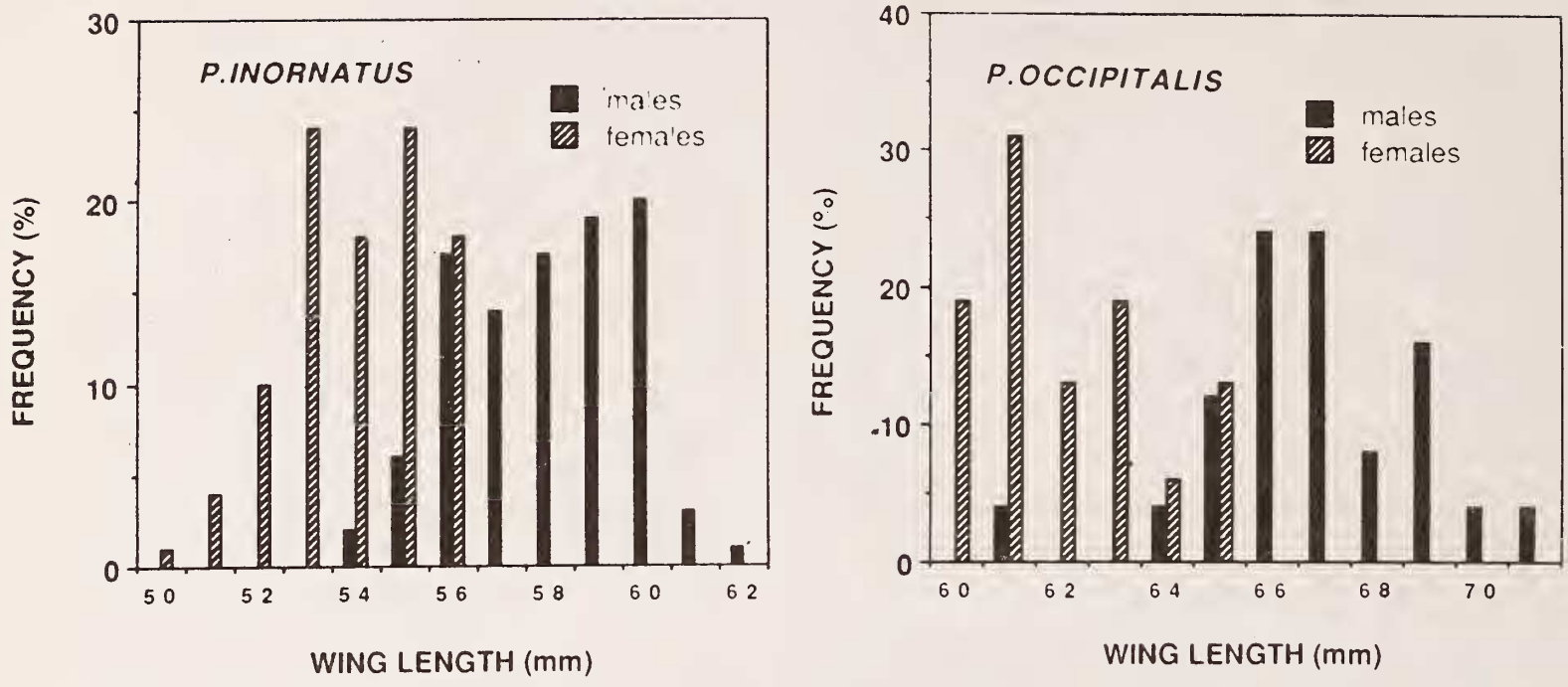

Fig. 2. Frequency histograms for wing length by sex.
Left: *P. inornatus* (N=64 males, 67 females). Right: *P. occipitalis* (N=25 males, 16 females).

TABLE 2

MORPHOMETRICS OF THE EIGHT SPECIES OF *Phylloscopus* WARBLERS STUDIED

Species	Wing length (mm) Mean ± S.D. (Min.,Max.)	Weight (g) Mean ± S.D. (Min.,Max.)	Tarsus (mm) Mean ± S.D. (Min.,Max.)	Beak length (mm) Mean ± S.D. (Min.,Max.)	Beak depth (mm) Mean ± S.D. (Min.,Max.)	Beak width (mm) Mean ± S.D (Min.,max.)	Sample size
P. tytleri	56.5± 2.2 (53.0,61.0)	7.2± 0.4 (6.3,7.8)	17.7± 0.6 (16.1,19.0)	6.2± 0.4 (5.0,6.8)	2.1± 0.2 (1.9,2.5)	2.2± 0.2 (2.0,2.6)	30
P. affinis/	56.2± 1.9 (53.0,58.0)	6.7± 0.6 (5.8,7.4)	18.7± 0.8 (18.2,20.0)	5.7± 0.3 (5.4,6.2)	1.9± 0.05 (1.9,2.0)	2.2± 0.1 (2.0,2.4)	5
P. pulcher	55.5± 2.6 (52.0,60.0)	6.4± 0.4 (5.9,7.3)	18.1 ± 0.8 (17.0,19.2)	5.3 ± 0.3 (5.1,5.8)	1.9 ± 0.1 (1.7,2.0)	2.3 ± 0.1 (2.1,2.5)	8
P. inornatus	55.9± 2.5 (50.0,62.0)	6.0± 0.4 (5.2,8.8)	17.5± 0.6 (15.9,19.1)	5.1± 0.2 (4.3,6.0)	1.9± 0.1 (1.7,2.3)	2.2± 0.1 (1.8,2.7)	228
P. proregulus	51.2± 2.6 (47.0,60.0)	5.1± 0.5 (4.2,8.5)	16.5± 0.6 (14.7,17.6)	4.7± 0.3 (4.1,6.9)	1.9± 0.1 (1.7,2.1)	2.4± 0.2 (1.9,2.8)	140
P. magnirostris	67.8± 3.3 (62.0,71.0)	10.0± 1.2 (7.4,11.1)	18.7± 0.5 (18.1, 19.5)	6.7± 0.6 (5.8,7.8)	2.8± 0.2 (2.4,3.0)	3.0± 0.2 (2.6,3.2)	8
P. trochiloides	62.5± 3.2 (57.0,67.0)	8.3± 0.7 (7.4, 9.7)	19.1± 0.7 (17.7,20.2)	6.3± 0.3 (5.9,7.1)	2.5± 0.1 (2.3,2.8)	2.9± 0.2 (2.6,3.4)	15
P. occipitalis	64.6± 3.0 (59.0,71.0)	8.7± 0.6 (7.3,11.2)	17.4± 0.6 (15.5,19.1)	7.0± 0.4 (5.9,8.2)	2.8± 0.1 (2.4,3.1)	3.1±0.2 (2.7,3.6)	99

Mean, standard deviation and range (in parentheses) are given. When individuals were captured and measured more than once their measurements were first averaged. The three beak measurements were taken from, or at, the front of the nares. The sample size varied somewhat among measurements and the smallest sample size is given.

Results

Description of the Species

Abundance and distributions: The *Phylloscopus* warblers are extremely abundant at Overa Sanctuary (Price and Jamdar 1990). Along a small valley through the fir woods at 2400 m 35% of all the small (< 150 g weight) Passerine individuals we caught were *Phylloscopus* warblers, while in the birch woods at 3300 m 43% were *Phylloscopus* warblers (Price and Jamdar 1990). In terms of biomass the corresponding figures are 18% and 23%. Besides the abundance of individuals there is also a high species diversity. All eight species are common, and at some localities in the Sanctuary, at about 3300 m, all species can be found breeding within a few hundred metres of each other (Price and Jamdar 1989).

We describe the altitudinal ranges and habitat preferences of each species in Appendix 1. Some species breed in very similar habitat — for example *P. trochiloides* breeds in birch along the treeline, overlapping completely with territories of *P. inornatus* and *P. pulcher.* Of the 28 total possible species pairs 8 (28%) have no contact with each other, while 7 (25%) have some territories which completely overlap. The remainder show partial contact (Table 1).

External appearance: The species are all very similar, being small, green above, and pale below. They differ externally in three ways: size and shape, plumage pattern, and song. We present biometrics of the eight species in Table 2. The largest species, *P. magnirostris,* is about twice as heavy as the smallest species, *P. proregulus,* and has a beak 40% longer (Table 2, Fig. 1). For the three species with sufficient sample sizes we present the measurements separately for each sex in Table 3. All three species are strongly sexually dimorphic in wing-length (with males 7-10% larger), as appears to be generally true in the *Phylloscopus* (Williamson 1974, Tiainen 1982), and possibly tarsus length, but not in body weight or the beak measurements. As in the European species (Tiainen 1982) it is possible to sex many individuals purely on the basis of wing length (Fig. 2). For example, in *P. inornatus* 75% of all the males and no females had wing lengths longer than 56 mm (Fig. 2).

Differences in plumage pattern arise from varying numbers of usually pale yellow patches on the upperparts (Williamson 1974). The patches are a superciliary stripe, bars on the greater and median coverts, a crown stripe, a

TABLE 3

MEASUREMENTS BY SEX FOR THREE SPECIES OF *Phylloscopus* WARBLERS.

	Wing length (mm)	Weight (g)	Tarsus (mm)	Beak length (mm)	Beak depth (mm)	Beak width (mm)	Sample size
	Mean± S.D.	Mean ± S.D.	Mean ±.S.D.	Mean ± S.D	.Mean ± S.D.	Mean ± S.D.	
P. inornatus:							
Males	58.0 ± 1.8**	6.0 ± 0.3	17.8 ± 0.6**	5.1 ± 0.2	1.9 ± 0.1*	2.2 ± 0.1	69
Females	53.9 ± 1.5	6.1 ± 0.3	17.2 ± 0.5	5.1 ± 0.2	1.9 ± 0.1	2.2 ± 0.2	66
P. trochiloides:							
Males	64.8 ± 2.0**	8.5 ± 0.6	19.7 ± 0.3	6.5 ± 0.5	2.5 ± 0.2	3.0 ± 0.3	4
Females	58.3 ± 1.0	7.8 ± 0.3	18.7 ± 1.1	6.1 ± 0.1	2.5 ± 0.1	3.0 ± 0.1	4
P. occipitalis:							
Males	66.9 ± 2.0**	8.6 ± 0.5	17.4 ± 0.6	7.1 ± 0.4	2.8 ± 0.2	3.1 ± 0.2	27
Females	62.3 ± 1.8	9.0 ± 0.8	17.6 ± 0.7	7.1 ± 0.5	2.7 ± 0.1	3.2 ± 0.2	18

Means, standard deviations and sample sizes are given. Only species for which at least four individuals of each sex were measured are included. Significance of the sex difference was assessed using *t* tests.**P<0.001 *P<0.05. All other differences were not significant.

TABLE 4

COMPOSITION OF NESTS

	Weight(g)	Grass	Lichen	Moss	Birch bark	Feathers	Hair	Sample size
P. tytleri	7	*	*	-	*	*	*	1
P. pulcher	19	*	-	*	*	*	*	1
P. inornatus [1]	17(12,25)	*	?	79	72	-	96	33
P. proregulus	10,12	*	*	-	*	*	-	2
P. occipitalis	14,15,23	66	-	*	33	–	66	3

[1]For *P. inornatus* the figures in parentheses after weight give the minimum and maximum weights recorded. *indicates every nest contained at least some of this material. The numbers indicate precentages of nests with a particular constituent. For all species the dominant constituent of the nest was grass, except for *P. occipitalis*, where it was moss.

rump patch, and white in the outer tail feathers. Two species — *P. tytleri* and *P. affinis* — have only the superciliary stripe, while one species *P. pulcher* has all the described patches. The others have intermediate numbers of patches (Williamson 1974). In *P. pulcher* the patches are distinctly orange, while *P. affinis* has bright yellow underparts.

All species sing characteristic songs. These songs have been described with sonagrams by Martens (1980). Three of the species – *P. pulcher, P. inornatus* and *P. proregulus* – sing two different songs (Martens 1980). We describe the context in which these songs are sung, and also previously undescribed call notes in a section below on the individual species. The general importance of song in speciation and mate recognition has been demonstrated in studies of European *Phylloscopus* (Thielcke *et al.* 1978, Helb *et al.* 1982).

Breeding Biology

In this section we contrast the breeding behaviour of the eight species. In many respects they are very similar. All build domed nests. Only the female incubates, while both parents feed the young. They differ in nest placement, nest materials, time of breeding, and slightly in

TABLE 5

CHARACTERISTICS OF NEST LOCATIONS FOR THE 8 *Phylloscopus* SPECIES

	tytleri	*affinis*	*pulcher*	*inornatus*	*proregulus*	*magnirostris*	*trochiloidse*	*occipitalis*
Hedgerow	1							
Juniper		5						
Birch	2		4					
Fir	2				8			
Rhododendron			6					
Ground or ledge				349		1	8	
Under stone								20*
Hole in tree								4
Tree cavity						1		7[1]
Rock cavity						1		1
Tree roots						2		1
Building wall								13
Total	5	5	10	349	8	5	8	46

* One nest was under a piece of wood on the ground.

1This includes 2 nests built under pieces of wood on fallen trees, and 3 predominantly in earth holes.

TABLE 6

MEDIAN FLEDGE DATES FOR *Phylloscopus* SPECIES AT THE HIGH ALTITUDE SITES

	1985	1986	1987
P. tytleri	—	—	19 Jul y(1)
P. pulcher	29 June (1)	23 July (2)	20 Jul y(1)
P. inornatus	28 June (54)	13 July(41)	10 July (55)
P. proregulus	—	—	22 Jul y(1)
P. magnirostris	20 July (2)	—	—
P. trochiloides	19 July (4)	27 July (3)	27 July (1)
P. occipitalis	8 July (5)	17 July (2)	20 July (3)

Median fledging date, with sample size in parentheses.

TABLE 7

DISTRIBUTIONS OF CLUTCH AND FLEDGE SIZES

	Number of eggs in clutch					Mean clutch size	Number of fledglings					Mean fledge size
	1	2	3	4	5		1	2	3	4	5	
P. tytleri					1	4.0		1				2.0
P. affinis					1	4.0						
P. pulcher			1	3		2.75		2	1			2.3
P. inornatus	5	13	46	170	19	3.73	5	16	32	54	11	3.4
P. proregulus										1		4.0
P. magnirostris							1	1	1	1		2.5
P. trochiloides		1	1	2		3.25		1	3	3		3.0
P. occipitalis		4	6	2		3.83			5	18		3.78

Shown are the number of nests containing each clutch or fledge size.

TABLE 8

MEASUREMENTS OF *P. occipitalis* AT THE LOW ALTITUDE (FRH) AND HIGH ALTITUDE (UP1) SITES

	Wing length (mm) Mean±S.D.	Weight (g) Mean± S.D.	Tarsus (mm) Mean± S.D	Beak length (mm) Mean± S.D	Beak Depth (mm) Mean±S.D.	Beak Width (mm) Mean± S.D.
FRH	65± 3.0	8.6± 0.6	17.3± 0.6	6.9± 0.3	2.8± 0.1	3.1± 0.2
UP1	65± 2.5	8.5± 0.6	17.9± 0.6**	7.1± 0.5	2.7± 0.1	3.0± 0.2

Sample sizes of birds measured are 59 at FRH and 11 at UP1. Significance between the two sites for each character was assessed by a two-tailed *t* test * $P < 0.05$ ** $P < 0.01$.

average clutch size. We have been unable to ascertain incubation and nestling periods for any species except *P. inornatus.*

Nest characteristics and nest placement: In most species the main construction material is grass, supplemented on the outer layers with moss, lichens and birch bark (Table 4). *P. occipitalis,* however, builds its nest almost entirely of moss. The lining differs among species. Of the five species whose nests we have carefully examined, three have always had feathers lining their nest, and two never have (Table 4). The difference between not using and using feathers corresponds with ground and hole nesters, which do not have feathers, but line with thin grass, mammal hair, or sometimes in the case of *P. occipitalis* do not line at all, and tree branch nesters, which use feathers, and also hair at least in some species (Table 5).

The difference may be related to the need

for greater insulation in trees (Moller 1984), but it is difficult to see what disadvantage there could be to ground nesters in using feathers. Moller (1984) suggests that the feathers make the nest more conspicuous, but this does not seem likely for species with domed nests. In addition, two species of European *Phylloscopus* studied by Tiainen *et al.* (1983) use feathers but nest on the ground. *P. pulcher* uses many feathers in its nest, and may place a feather 'door' across the nest entrance, as has been observed for *P. collybita* and *P. trochilus* in Finland (Tiainen *et al.* 1983).

Nest locations: Most species show characteristic differences in their choice of nest location (Table 5). Two species (*P. inornatus* and *P. trochiloides*) nest on the ground, and use similar sites (the nests also appear similar, except for the larger size of that of *P. trochiloides* whose nest we have not examined in detail). *P. occipitalis* uses a variety of nest sites, including holes in earth banks, rocks, buildings, and trees (where they have been recorded up to 10 m by us) and under stones and fallen pieces of wood. We have recorded *P. tytleri* nesting in birch (at 8 m), in a hedgerow (at 2 m), and in a fir tree (at 15 m). Like *P. proregulus,* the nest is built among thin branches. *P. pulcher* either builds a nest among the thin branches of a rhododendron, where it can be quite conspicuous, or in a cavity on a sturdy branch of a birch tree.

Time of breeding: Timing of breeding is examined in Table 6, using the average day on which the nestlings fledge. Use of fledging date confounds variation in incubation and nestling period with date of laying, but our observations on eggs and young of several species, while not providing exact information on the incubation and nestling periods, lead us to believe that they are similar among species.

In *P. inornatus,* which breeds early, incubation period can vary from 12-22 days (Price and Jamdar 1991); such variation is unlikely in the other species which breed later in more favourable conditions. We show in a later section that for *P. occipitalis* timing of breeding varies with altitude, hence we consider only observations at the high altitude camps (where apart from some *P. occipitalis* and one *P. magnirostris* nest all nests with fledglings were found).

Time of fledging appeared to vary among years for all species, but, given the small samples, significantly only in the case of two species; *P. inornatus:* $F(2,147)=143, P<0.0001$; *P. occipitalis:* $F(2,7)=41, P<0.001$. In 1985 all species bred earlier than in the other two years, presumably because of the better weather in that year (Price and Jamdar 1990).

In each year we found significant variation in time of breeding among the species; 1985: $F(4,59) = 25, P<0.0001$; $F(3,60) = 10, P<0.0001$; 1987: $F(5,48)=3.0, P<0.05$. *P. inornatus* bred the earliest, and *P. magnirostris* and *P. trochiloides* the latest. For several species sample sizes are small, but the timing of breeding agrees broadly with our many observations on nest building and on nests containing eggs (sample sizes in Table 5) and on post-breeding family parties. The exception is *P. pulcher,* which (based on nest building) may have on average bred earlier in 1986 than our two fledging dates indicate.

Clutch and fledge sizes: Clutch sizes for all species are presented in Table 7. For several species we have small samples, and we suspect the average clutch represented by the *P. pulcher* sample is atypically low for that species. Apart from *P. pulcher* four is the commonest clutch size for all species. Similar values for clutch sizes have been presented by Hume and Oates (1889) and Baker (1933). Clutch sizes are lower than the six or more commonly recorded for European species of *Phylloscopus* (Tiainen *et al.* 1983).

Predation: We have noted nest predation as having occurred on all species except *P. tytleri.* A list of known predators is given by Price and Jamdar (1991). We have actually observed the following predation events: nutcracker *Nucifraga caryocatactes* on *P. inornatus* and *P.*

pulcher (nests with eggs); Himalayan viper *Agkistrodon himalayanus* on *P. occipitalis* (nest with fledglings). Much predation was attributable to an unnatural abundance of crows and some of it to crows following us. Hence it is impossible to determine a natural rate of predation, or to look for differences among the species in association with their nesting habits.

Nest parasitism: Nestlings of *P. occipitalis* commonly have fly larvae, presumably of the genus *Protocalliphora* (Owen 1954) up to 1 cm long attached to their feet, and more rarely their head. We did not keep detailed records, but have noted up to five on one nestling. Infested nestlings appeared healthy, and fledged successfully. The highest altitude at which we have observed these larvae is at 2800 m at Kanj Kut and we have not found them at the high altitude sites, or on any other species.

Three species of cuckoo *(Cuculus)* are present in the study area (Price and Jamdar 1990). All have been recorded as brood parasites of *Phylloscopus* species (Ali and Ripley 1983). In fact we found a single case of brood parasitism: a *P. affinis* nest with a young small cuckoo *Cuculus poliocephalus* in it. We did not find any evidence of brood parasitism in more than 200 nests of *P. inornatus,* despite the small cuckoo being common where it breeds. This suggests that *P. inornatus* is a 'rejector species' (Brooke and Davies 1987) and will not incubate cuckoo eggs.

Observations

The purpose of this section is to present information on those species which differs from, or adds to, that in the current literature (Gaston 1974, Williamson 1974, Martens 1980, Ali and Ripley 1983).

Phylloscopus tytleri: Alexander (1950) mistook this species for *Phylloscopus neglectus,* which has not been recorded by us or any other observer in Kashmir, and Alexander's error was perpetuated by Ali and Ripley (1983). Thus the song *ti wish i* which is attributed to *P. neglectus* by Alexander is clearly the *let's kiss him* phrase aptly coined by Osmaston (1927) to describe the song of *P. tytleri* (see also the sonagrams of Martens 1980). We have never heard a song resembling the *whittle di wee you* which Alexander attributed to *P. tytleri.*

The call note of *P. tytleri* does not seem to have been recorded by previous workers: it is a plaintive *sooeet.* It is not often heard at the beginning of the breeding season, but is uttered when an observer is around the nest and is very common in July, particularly when the birds are in family parties after the young have fledged.

P. tytleri has a long and slender bill (Williamson 1974; Table 2). We suspect that this may enable it to probe flowers for insects and/or nectar and pollen. We caught several individuals with red pollen on their chins and foreheads.

***Phylloscopus affinis*:** This species breeds at higher altitudes than the others, and is *a priori* more likely to be susceptible to late inclement weather. Although in both 1986 and 1987 birds were singing on territory by mid May, we also observed a male singing at Overa village on 3 June 1986, suggesting that birds leave their territories if the weather is bad and/or some birds arrive late. We have no information on fledging date, but have observed nest building in the first two weeks of June, and found a nest with eggs on 27 June 1986. We also found one nest with a well developed small cuckoo chick in it on 13 July 1985. This implies that fledging may occur in mid-July, and that *P. affinis* does not breed much later than some of the other species (Table 6).

Phylloscopus pulcher: Each male sings two songs (Martens 1980). The first song is a hard *tick tick tick* followed by a trill and the second a musical *dioo dioo..,* for about eight repeats of the *dioo.* The songs appear to be used in different contexts. The first song is heard throughout May when the weather is fine. It is sung by males seen foraging in areas 100-200 m below their future territories (they are commonly seen down to 3300 m prior to breeding, al-

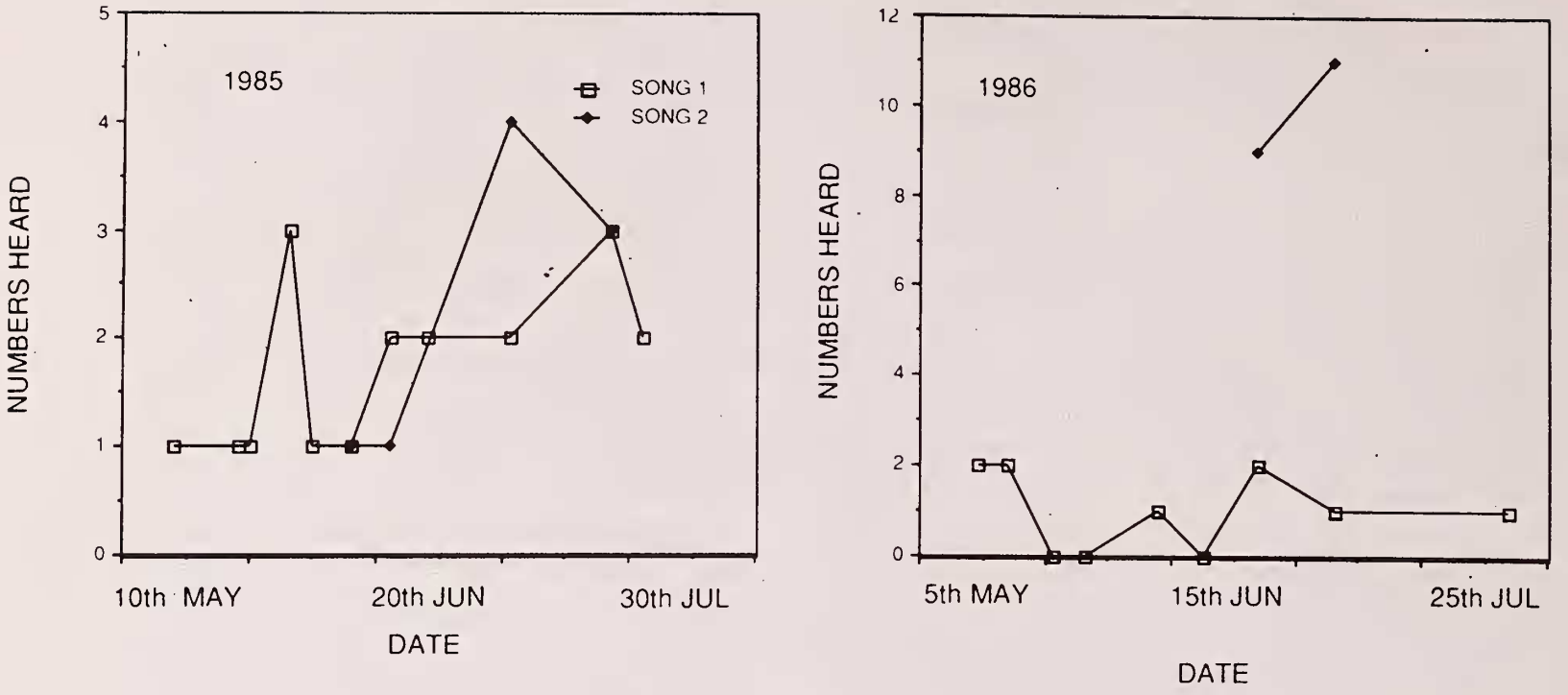

Fig. 3. The numbers of *P. proregulus* singing each of the two song types, observed on a 2 km post dawn walk along a valley through coniferous forest, conducted at irregular intervals in 1985 (left) and 1986 (right). Song 1 is the trill song, Song 2 is the long rambling song (see text).

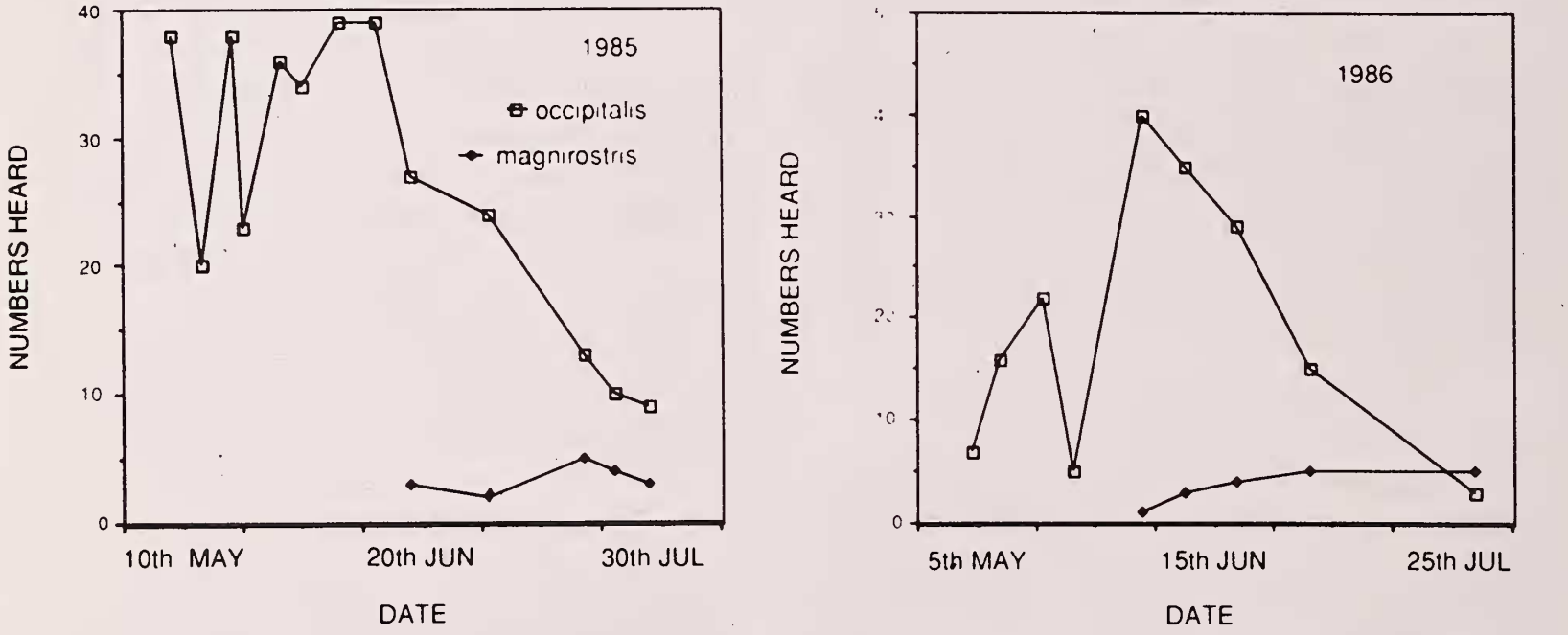

Fig. 4. The numbers of *P. occipitalis* and *P. magnirostris* singing, observed on the post dawn walk through coniferous forest.

though we have not recorded them lower). The second song is heard intermingled with the first, but it is only sung by males on territory. In 1986 it was first heard on the 11 June, and in 1987 it was first heard on 3 June.

Phylloscopus inornatus: We made a special study of this species and the results are reported in a separate paper (Price and Jamdar 1991).

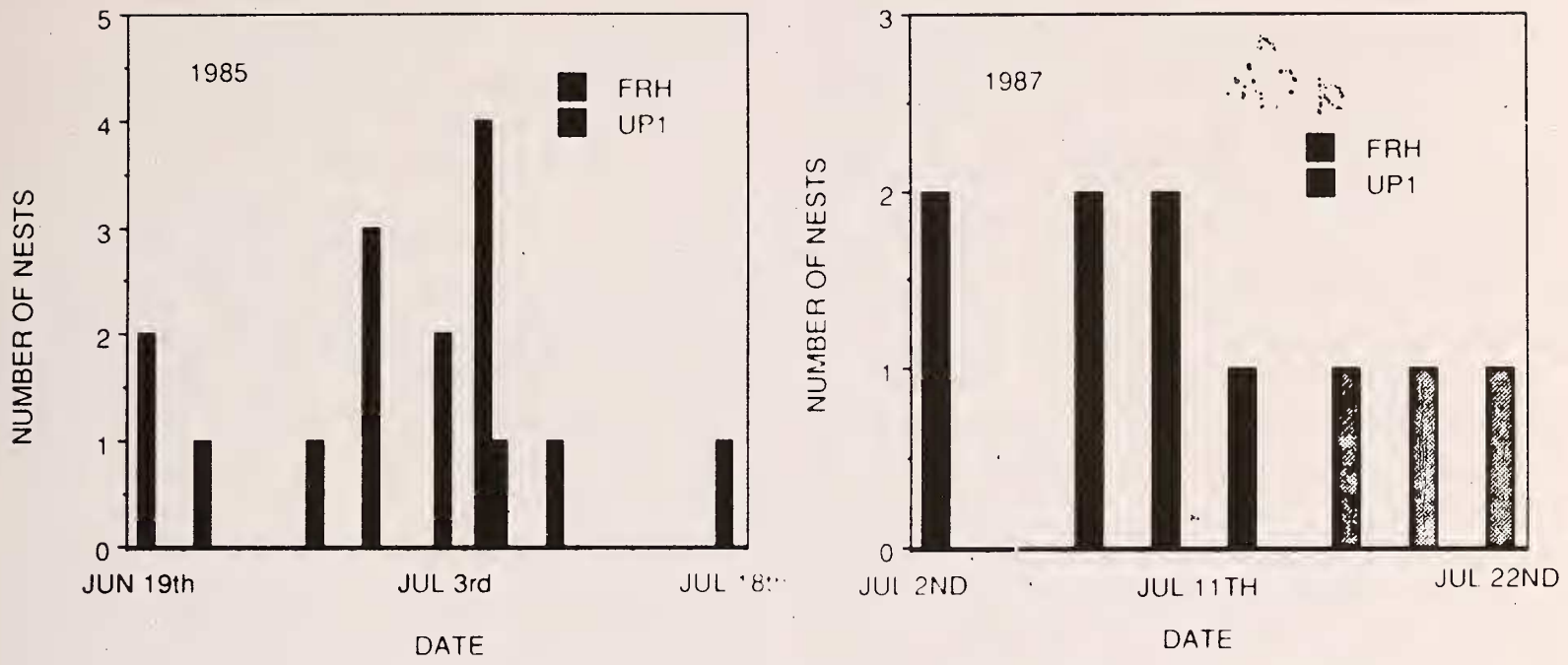

Fig. 5. Distributions of fledging dates for *P. occipitalis* at *c.* 2800 m altitude in fir forest (FRH) and *c.* 3200 m altitude in birch forest (UP1). Above: 1985 (Median date at FRH=July 1; at UP1=July 8; *t* test for significance of means, t=2.3, N=16, p< 0.05). Below: 1987 (Median date at FRH=July 7; at UP1=July 20; t=4.7, N=10, p< 0.01).

Males sing two songs. We also noted rare distinct songs. In particular one individual sang a long (> 1 minute) rambling warble.

Phylloscopus proregulus: Prior to breeding, and sometimes when the weather deteriorates early in the breeding cycle, birds may be found in large flocks of sometimes more than 100, feeding commonly in the undergrowth as well as in conifers. These flocks often contain a few tits *Parus* spp. and goldcrests *Regulus regulus*.

Males sing two songs. One is a thin trill preceded by a *tit tit tit*, similar but much weaker than the song of *P. pulcher*, and the other is a long rambling song of chirps and twitters lasting up to 15 minutes or more (Martens 1980). This song is often uttered from the top of a very tall fir tree, although we rarely heard snatches from males foraging close to the ground. The first song can be heard whenever the sun shines at least from the beginning of May (when our study began each year). The second song is only heard when nesting begins (it was first heard on 31 May 1985, and 3 June 1986), and like the second song of *P. pulcher* appears to only be uttered on territory. The number of each kind of song heard on a post-dawn 2 km walk through fir forest at *c.* 2500 m are displayed in Fig. 3.

Phylloscopus magnirostris: The species is one of the last to arrive in the Overa Sanctuary each year (Fig. 4 of Price and Jamdar 1990). One nest site was known to have been used in two successive years; two others were not.

Phylloscopus trochiloides: Although the species breeds late, males can be heard singing at low altitudes (e.g. at the Forest Rest House) from early May. Many guide books suggest that *trochiloides* and *magnirostris* are best distinguished by the hook on the upper mandible of *magnirostris*. We have not found this to be a good character. In particular, many *trochiloides* show a hook. More diagnostic is the colour of the base of the lower mandible: yellow in *trochiloides* and pink in *magnirostris*.

Phylloscopus occipitalis: This species breeds commonly through the Sanctuary (Appendix 1). In Table 8 we record the average measurements

of birds caught at two altitudes (and in two different habitats). Individuals in the birch forest at high altitude have longer tarsi and thinner bills than those in the fir at lower altitudes. The birds at low altitude also breed one to two weeks earlier than those at high altitude (Fig. 5). The bases for the differences in morphology and laying date are unclear, but earlier fledging may reflect the better climate earlier in the season at the lower altitude (Price and Jamdar 1990).

Nevertheless, in other bird populations both laying date and morphology are known to be partly under genetic determination (Schluter and Smith 1986, Price *et al.* 1988) and it is possible that there is some genetic differentiation along the altitudinal gradient. The situation merits further investigation. Microgeographic variation in the European *P. trochilus* has been recorded. Ebenman and Nilsson (1981) found that *P. trochilus* on small Swedish islands were smaller in body weight than those on the nearby mainland. Tiainen (1982) showed that male *P. trochilus* are larger in wing length in coniferous than deciduous areas. He did not measure beak characters, and wing length increases with age (Hogstad in press), so his observations may not be comparable with ours.

Although Hume and Oates (1889) stated that the nests of this species are difficult to find. Bates and Lowther (1952) stated that it was 'impossible not to find' numbers of *P. occipitalis* nests, particularly in the fir woods. We have not found it easy to locate nests in this habitat, and suspect that pairs may be using tree cavities and holes quite high above the ground, as we observed on a few occasions.

Our assistants have recorded *P. occipitalis* singing in Overa village by the first week of April. It is common in the Sanctuary before we arrive in May and sings on every fine morning (Fig. 4). Song declines when most of the young have fledged. Apart from the call notes described by Ali and Ripley (1983) there is a call — a nasal *cheeze* — which we have only heard twice: both times when a cuckoo *Cuculus canorus* was near a nest early in the season. The young when fledged have an unusual begging call consisting of a several note chatter.

When ringing young at a nest we once observed dramatic injury feigning by one parent. This is the only record of injury feigning we have in the *Phylloscopus*. In many hours of observation on Darwin's ground finches one of us (T.P.) similarly recorded just one instance of injury feigning (by a cactus finch *Geospiza scandens*, unpublished observations). Such isolated observations suggest that injury feigning as a distraction display may have arisen very early in bird evolution.

Status of *P. reguloides*: A ninth species of *Phylloscopus, P. reguloides,* is listed as occurring in the Vale of Kashmir (Ali and Ripely 1983). *P. reguloides* is the only crowned leaf warbler occurring in Nepal. There are few differences between *P. reguloides* and *P. occipitalis* (Williamson 1974, Ali and Ripley 1983). Sonagrams of songs appear similar (Martens 1980), and the main external difference between them was listed as the extent of white on the third outer tail feather by Williamson (1974) and Ali and Ripley (1983). From examination of museum specimens at the British Museum this did not appear to us to be a good character. Evidence for breeding of *P. reguloides* in Kashmir comes from just two records published before 1910 (Ali and Ripely 1983), and it is largely this evidence (i.e. sympatry with *occipitalis*) which has been used to justify two species. We are convinced that only one species of crowned leaf warbler (i.e. *P. occipitalis*) breeds in the Vale of Kashmir, and think it possible that *P. reguloides* and *P. occipitalis* are in fact conspecific.

Discussion

The main purpose of this paper has been to describe the breeding biology of the leaf warblers occurring in Kashmir. Much of our information agrees with, and extends, that summarised by Williamson (1974) and Ali and

Ripley (1983). However, our observations differ from published information in a number of ways. For example, the habitats occupied by three of the eight species are not those suggested by Gaston (1974) in his investigation of morphology-habitat associations.

The inconspicuousness of these species together with their extreme similarity has resulted in them being ignored by many field workers. There is still a great deal that needs to be learned (for example, incubation and nestling periods are unknown for all species except *P. inornatus*) and many of our observations are based on small sample sizes. Some species (*P. tytleri, P. occipitalis*) are generalists in their range of habitats occupied and placement of nests; the others are more specialised. While generalists are more widely distributed over the altitudinal gradient, there is no good association between abundance and degree of habitat specialisation (*P. tytleri* is one of the less common species, Price and Jamdar 1990).

Differences in morphology, altitudinal range, habitats occupied, timing of breeding, plumage pattern, and song may all enable similar species to coexist in the breeding season. It is very difficult to assess the relative importance of these factors, and the extent to which they are products of species interactions (i.e. examples of character displacement) or incidentally selected (Grant 1972). Some are considered further by Price (in prep.). There are also differences in nest placement and nest construction, and it has recently been suggested that these differences could also promote coexistence through the agency of predation (Martin 1988a, in press). Martin (1988a) showed experimentally that if artificial nests were placed all on the ground or all in the trees they suffered higher nest predation than if some were placed on the ground and some in trees, apparently because predators localise their search. Thus two species could both increase their nesting success by one nesting on the ground and one in trees. Martin's hypothesis that the species are partitioning nesting space seems inapplicable if ground nesters have higher predation rates than tree nesters, because any individual of the ground nesting species which nested in a tree should be selectively favoured.

In some localities *P. pulcher* nests in trees while *P. trochiloides* and *P. inornatus* nest on the ground. At other localities *P. tytleri* and *P. proregulus* nest in the trees while *P. inornatus* nests on the ground. While we do not have comparative rates of predation, several predators are ground specialists, such as the Himalayan weasel *Mustela sibirica* and the viper. It seems likely to us that predation rates are higher on the ground nesters, as has been widely observed in other studies (summarised by Martin 1988b). In addition, at both the localities mentioned the ground nesters are far more abundant than the tree nesters, making density-dependent predator specialisation on ground nesters more likely. Hence the idea that species partition nesting space solely in response to predation seems unlikely. Nest parasitism and other factors affecting reproductive success may be important.

Many questions need to be addressed before we can assess the factors contributing to the abundance and species diversity of this genus in Kashmir. We tentatively suggest that resource and habitat partitioning in the non-breeding season will be found to be of major importance. If this is the case then studies of the changing abundance of these warblers in Kashmir should provide useful environmental indicators as to the state of habitat both in Kashmir, and in the plains of India, where all the species pass their winter.

Summary

We describe the breeding and other characteristics of eight species of leaf warblers (genus *Phylloscopus*), at Overa Wildlife Sanctuary, Kashmir, based on three summers (1985-1987) of study. The species are similar, and differ by a maximum of two-fold in body weight. They are sexually dimorphic in wing length, but

monomorphic in beak characters and body weight. For *P. occipitalis* (which breeds throughout the Sanctuary) individuals at high altitudes have longer tarsi and slimmer beaks than those at low altitudes. The species differ in plumage pattern and song. Three species sing two different songs.

Some species have strict habitat preferences, whereas others are more generalised, and altitudinal ranges vary accordingly. They all build domed nests: some build in trees, and others on the ground, while one (*P. occipitalis*) breeds in holes and cavities on the ground and in the trees. For each species timing of breeding differs among years in relation to the weather. *P. occipitalis* individuals at low altitude breed earlier than those at high altitude. Within each year there is about a two week difference in the average time of breeding of the first and last species to breed.

A number of factors could contribute to the high diversity and abundance of *Phylloscopus* species in Kashmir. With current data we are unable to assess most of these, but we tentatively reject nest predation as being important in leading to species coexistence.

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APPENDIX 1

TERRITORY CHARACTERISTICS AND ALTITUDINAL RANGES OF THE EIGHT *Phylloscopus* SPECIES

P. tytleri, Tytler's warbler. This species breeds in hedgerows around Overa village (at 2300 m), in fir trees on the forest edges throughout the Sanctuary, and in the pure birch as high as 3350 m. It is not found in pure coniferous woodland (cf. Gaston 1974). It is most abundant in forest clearings at *c.* 2800 m. In July individuals forage in the juniper above the tree-line.

P. affinis, Tickell's leaf warbler. The species breeds only in juniper, hence it occurs from *c.* 3300 to above .300 m, although it is regularly seen at lower altitudes in May.

P. pulcher, orangebarred leaf warbler. Every territory of this species (more than 30 males observed) has contained rhododendron bushes. The species occurs close to the treeline, where rhododendron is most abundant (3400-3600 m). All but one territory has also contained birch, but pure birch and areas with few rhododendrons (e.g. at 3300m at UP1) are not occupied.

P. inornatus, yellowbrowed leaf warbler. Every territory of this species has contained birch trees (more than 300 territories observed), hence it occurs from c. 3100 to c. 3600 m (tree line). Many territories may contain many conifers, but pure conifer stands are not occupied.

P. proregulus, Pallas's leaf warbler. Breeds only in coniferous trees, and occurs commonly throughout the coniferous woodland from where they start in the Sanctuary at *c.* 2300 m. Some pairs breed in isolated tall firs surrounded by predominantly birch trees (in which they forage) as high as 3350 m.

P. magnirostris, largebilled leaf warbler. Intimately associated with watercourses, and occasionally dry valleys, from *c.* 2400 m up to *c.* 3300 m. Forages in both birch and conifers.

P. trochiloides, dull green leaf warbler. Occurs in birch mostly at the treeline, but recorded as low as 3300m. Apparently breeds only in the wetter areas.

P. occipitalis, large crowned leaf warbler. Occurs from Overa village (*c.* 2300 m), where it breeds in houses, throughout the coniferous woods, and also in the birch up to *c.* 3350 m. It breeds close to, but not right at the treeline.

NOTE.- Based mainly on casual observations of at least 30 territories for each species.